

TWO GYNANDROMORPHOUS ANTS

BY WILLIAM MORTON WHEELER

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Two gynandromorphous ants which have turned up in recent collections are of unusual interest since they differ significantly from any of the similar anomalies previously described. One is a gynandromorph in the strict sense of the term, *i. e.*, a combination of the female and male of our common *Lasius* (*Acanthomyops*) *latipes* Walsh, the other a dinergatandromorph, or combination of the soldier (dinergate) and male of a Philippine ant, *Camponotus* (*Colobopsis*) *albocinctus* Ashmead.

For many years I have been expecting to find a gynandromorphous *Lasius*, both because the species of this genus are among the commonest and most widely distributed Eurasian and North American ants and because it seemed to me that at least an ergatandromorph, or combination of worker and male characters might occur as readily as in other ants, since these two phases in *Lasius* are of about the same size. On September 21, 1917, while turning over a large stone at Colebrook, Conn., in a pasture less than a quarter of a mile from the spot in which I took the gynandromorphous Mutillid described in a former number of PSYCHE,² I found a compact cluster of about two hundred of the bright yellow workers of *L. latipes* and in their midst a black insect, which I took to be an unusually large male. I placed the specimens in a vial of strong alcohol and continued my collecting. On returning home I was surprised to find that the dark specimen was a remarkable gynandromorph of a *Lasius* in which the sexual differences are more extreme than in any other species of the genus or indeed of any of the North American ants, except the Ecitons. Many years ago McClendon and I³ endeavored to show that *L. latipes* is peculiar

¹ Contributions from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 153.

² A Gynandromorphous Mutillid. PSYCHE 17, 1910, pp. 186-190, 1 fig.

³ Dimorphic Queens in an American Ant (*Lasius latipes* Walsh). Biol. Bull. 4, 1903, pp. 149-163, 3 figs.

in possessing two forms of females, one, which we called the β -female, being reddish-yellow, with long golden pile, large, flattened femora and tibiae, short, slender tarsi and incrassated antennae; and one, which we called the α -female, of a darker color and intermediate in structure and pilosity between the β -female and the female of *L. claviger* Roger.¹ The gynandromorph taken at Colebrook is evidently a combination of the male and β -female. These phases, when they appear as separate individuals measure respectively 4 and 8 mm., and could hardly be combined to form a viable lateral gynandromorph, so that it is probably for this reason that the specimen, as will appear from the description and figure, is of a different type. Unfortunately I did not have access to a dissecting microscope till the specimen had become so thoroughly hardened in the alcohol that I despaired of gaining any satisfactory knowledge of its internal reproductive organs. The gynandromorphous *C. albocinctus* was found among a small series of dried and mounted specimens collected for me in 1917 by Dr. F. X. Williams at Los Baños, near Manila. The following detailed descriptions and the figures will give an idea of the external peculiarities of the two specimens.

***Lasius (Acanthomyops) latipes* Walsh (Fig. 1)**

Gynandromorph. Length 8 mm., being that of the normal β -female, but with the thorax and gaster more slender. Head shaped like that of a normal female, but with the eyes and ocelli much larger and more prominent, the right posterior ocellus smaller than the left and the surface black, with isolated, reddish-yellow spots as indicated by the less densely stippled areas in the figure. Left mandible of the female type, reddish-yellow, smooth, shining, sparsely punctate; right mandible black, like the left in form and size but subopaque and very finely longitudinally striolate as in the male. Clypeus with somewhat more than its right half reddish-yellow (female), the remainder black (male). Antennae both alike, black, 13-jointed (male) and with slightly swollen first funicular joint but stouter than in the male, in form only slightly approaching the female, as in normal individuals of this sex the scape is incrassated distally and the funiculus is spindle-shaped, with very broad and transverse joints in the middle. The surface

¹ These females are figured in the paper cited and in my ant book (Fig. 55 B and C, p. 94).

of the head is subopaque as in the male and not smooth and shining as in the female, but the pilosity is long as in the latter though the hairs are dark and not golden as in the female. Thorax similar to that of the female but the pro- and epinotum are somewhat narrower and the former is asymmetrical, being shorter on the left than on the right side so that the head is turned to the left. The mesonotum and scutellum are more like those of the male. The thorax is black and has the same sculpture and short, sparse

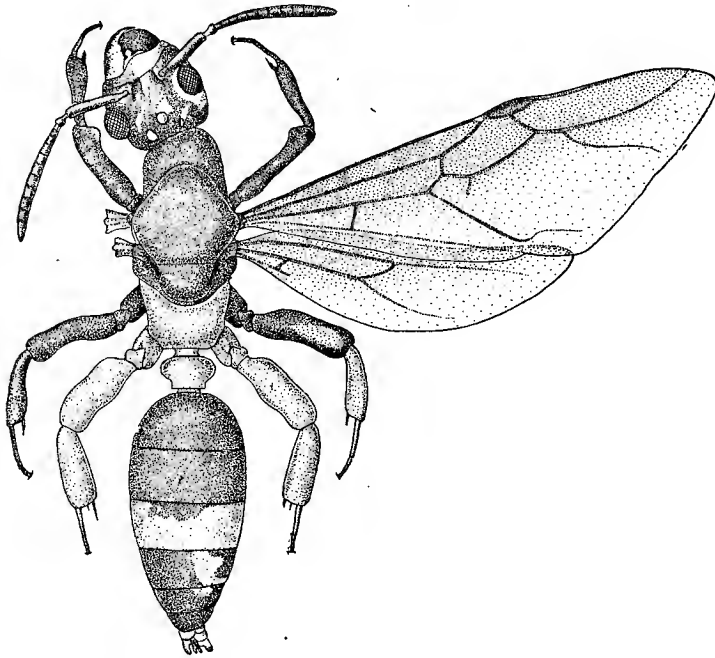


Fig. 1. Gynandromorph of *Lasius* (*Acanthomyops*) *latipes* Walsh.

pilosity as in the male, with the exception of the epinotum, which is reddish-yellow and has the long, abundant, golden hairs of the female. The petiole, too, is entirely of the female type in shape, color and pilosity. The gaster is narrower and more pointed posteriorly than in the normal female and with six visible segments and therefore more nearly of the male type. Its first and second segments are entirely black above (male), the third reddish-yellow (female), except for a black, asymmetrical transverse blotch at the

anterior border on the dorsal surface; the fourth, fifth, and sixth segments are black (male), but the fourth has an irregular reddish-yellow band extending over its full length on the right side above, and the fifth has a small spot of the same color on the same side at the anterior margin. On the ventral side the first segment is black throughout, the second with an oblique reddish-yellow blotch to the left of the median line, the third with a narrow black longitudinal streak in the middle and a large rounded black spot on the left posterior corner. The fourth ventral segment is entirely black and very small, the fifth yellow. External genitalia of the male type, much as in normal individuals but more robust and turned somewhat to the right side. Sculpture, pilosity and pubescence of the gaster as in the male. Legs very peculiar in that the hind pair, including their coxæ, are of the normal female form, pilosity and color, whereas the right fore leg and left middle leg, including their coxæ, are entirely black and in form intermediate between the male and female types though somewhat more like the latter in form and size. Left fore leg black on its extensor and reddish yellow on its flexor surface and more nearly like the normal female fore leg in form than the right fore leg. Right middle leg much more like that of the female than the left middle leg, the coxæ and femur black, the latter with a long fusiform reddish-yellow spot on its extensor surface, the tibia and tarsus reddish-yellow throughout as in the female. The pilosity on the legs is short and sparse (male), except along the flexor border of the left fore tibiæ and on the hind legs where the hairs are long and of the female type. Both pairs of wings are normally developed and in size and shape as in the female, but the hind pair dropped off readily soon after the specimen was placed in alcohol, whereas the fore pair remain firmly attached, showing a pronounced tendency to deâlation (female) only in the metathoracic articulations. The fore pair has the posterior half of the recurrent vein absent. This reveals a condition half way between those of the normal female and male, since in the former the recurrent vein is complete and closes the discoidal cell, whereas in the male it is usually entirely absent so that the wing is without a discoidal cell.

The unusual interest of the specimen lies in the fact that it cannot be placed in any of the categories of gynandromorphs, for as a whole it belongs neither to the more frequent lateral, nor to the

rarer anteroposterior, decussating, mosaic or blended types, but exhibits a mixture of all of them. The mandibles and clypeus have the sexual characters of the lateral type but the arrangement of colors in the clypeus is the reverse of that of the mandibles and hence decussating. The head is female in form but partly blended, partly mosaic and feebly lateral. The eyes, antennæ, anterior ocellus and left posterior ocellus are strongly male. The right posterior ocellus, the right eye, which is distinctly smaller than the left, and the large area of reddish-yellow integument surrounding it, show that the right side of the head is more female than the left. The thorax in front of the epinotum is a blend of male and female characters, the pronotum being more female, the mesonotum and scutellum more male as are also the color, sculpture and pilosity of these three regions, whereas the epinotum and petiole are purely female. The wings are female but with the female tendency to dealation only in the hind pair and the reverse or male tendency to persistence in the articulations of the anterior pair. But the latter show in the retention of the anterior half of the recurrent vein a very interesting condition precisely half-way between that of the normal male and female wing. The hind legs are purely female but the two anterior pairs show a peculiar decussation, the left fore and right middle leg being more female in form and coloration and the right fore and left middle leg more male. This decussation of characters is similar to that of the mandibles and clypeus but less pronounced. It is very probable that the internal reproductive organs are more or less hermaphroditic, as they are situated in segments which externally exhibit a very striking mosaic of male and female characters.

Camponotus (Colobopsis) albocinctus Ashmead (Fig. 2c)

Dinergatandromorph. Length 4 mm.

In all respects like a normal soldier, except in its smaller size (the normal soldier measures about 5 mm.) and in having the head asymmetrical, with its smaller right half exhibiting male characters. The right eye is larger, more convex and nearer the middle of the side of the head than the left. The right antenna is 13-jointed, with the terminal joint short and aborted, and the right mandible, though much shorter than in the male (Fig. 2a) has only two teeth separated by a wide concavity of the apical border. The clypeus on the right side has the lateral extension characteris-

tic of the male and the same type of frontal carina, whereas the left frontal carina is prolonged backward as in the soldier (Fig. 2^b) but does not border so deep a scrobe-like depression. In the soldier the head is ferruginous or yellowish-red, with its posterior third infuscated, but in the male entirely black. In the dinergatandromorph the infuscation extends much further forward between the frontal carinae and onto the right side. There are no

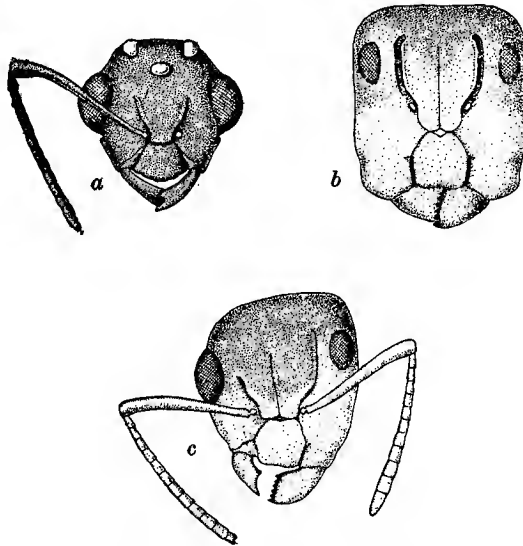


Fig. 2. *Camponotus (Colobopsis) albocinctus* Ashmead. a, head of male; b, of soldier; c, of dinergatandromorph.

traces of ocelli. As the thorax, petiole, gaster and legs are in all respects like the corresponding parts of a normal though small soldier the internal reproductive organs are, in all probability, those of a normal soldier, *i. e.* of the abortive female type.

I have not seen the worker of *C. albocinctus* but there can be no doubt that as in other species of the subgenus it has a small head, more rounded, less rectangular and narrower in front than in the soldier, with less convex mandibles and the clypeus shaped more as in the male. The species of *Colobopsis* are peculiar in having sharply marked soldier and worker forms, whereas in other subgenera of *Camponotus* the workers are polymorphic, *i. e.* form a more or less evenly graded series from maximal to minimal in-

dividuals. To my knowledge this is among ants the only known gynandromorph that exhibits an unmistakable combination of male and soldier characters. In other cases the male characters are combined either with the worker or with the female. Even the lateral gynandromorph of *Camponotus ligniperda*, described and figured by Klapálek,¹ represented a combination of the male and worker minor.

The dinergatandromorph of *C. albocinctus* seems to me to be very significant in connection with the previously known thirty Formicid gynandromorphs and the *Lasius latipes* described above.² It is evident that the male characters may be combined not only with the female as in the gynandromorphs of other animals, but also with the soldier and worker. And although the latter are abortive females, they nevertheless behave in combination with the male like entities quite as distinct and independent as the fertile female. This suggests that the worker and soldier are not products of nutrition but are germinally predetermined. In other words, it would seem that in ants with male, female and worker castes, we must postulate three, in species with a soldier caste, four different kinds of eggs. This view is also supported by the following considerations: first, Bugnion and Miss Thompson have shown that in termites, which have developed castes surprisingly like those of ants, the soldiers, workers and sexual forms can be recognized as distinct *on hatching from the egg*; second, embryological study has shown that the insect egg is the most precociously specialized of all animal ova, so specialized, in fact, that not only the anterior and posterior poles but also the dorsal and ventral and right and left sides of the organism that is to arise from it are morphologically predetermined even before the extrusion of the polar bodies; and third, artificial castration has shown that operations on the primary sexual characters of young insect larvæ fail to disturb the development of the secondary sexual characters and instincts.

All these considerations point to the conclusion that in such very ancient and extremely specialized organisms as insects, sex and caste peculiarities have been impressed on the organization of the

¹ Obojetnik *Camponotus ligniperda* Latr. Sitzb. Böhm. Ges. Wiss., 1896, 4 pp., 2 figs.: Wheeler, Some New Gynandromorphous Ants, with a Review of the Previously Recorded Cases. Bull. Amer. Mus. Nat. Hist. 19, 1913, p. 675, Fig. 11.

² Reviews of the known cases are given in my papers: Some New Gynandromorphous Ants, etc., *loco citato*, pp. 653-683, 11 figs. and Gynandromorphous Ants Described during the Decade 1903-1913. Amer. Natural, 48, 1914, pp. 49-56.

very young egg and are not determined by fertilization or by the incidence of trophic stimuli during larval development. I was, therefore, led in my first paper on the ant gynandromorph to postulate its origin from a pair of fused oöcytes. The difference between the various types of gynandromorphs—lateral, frontal, mosaic, blended, etc.—was supposed to be due to the differences in the two kinds of ova, the plane of their fusion, regulatory tendencies that would avoid reduplication of organs, and differences in growth in the component ova or their parts to account for such cases of imperfect lateral gynandromorphs, as *e. g.* that of the *Camponotus albocinctus* described above, in which the male is so much smaller than the soldier component. My views have been treated as rankly heretical by Boveri¹ and his pupil, Fräulein Elsa Mehling,² but Cockayne,³ who has recently made a comprehensive study of Lepidopteran gynandromorphs, while pointing to certain defects in my hypothesis, remarks that "it explains better than any other how in heterochroic gynandromorphs the areas occupied by the two colors and two sexes are identical." He also mentions with approval the fact that "Doncaster has recently suggested that a gynandromorph is produced by the fertilization of each of the nuclei of a binucleate ovum by a separate spermatozoon. He has proved the existence of these binucleate ova and has actually proved the conjugation of a separate spermatozoon with each and seen the resultant mitoses." I should, of course, regard such a binucleate ovum as the first result of the fusion of two ova. The hypothesis of Boveri and Fräulein Mehling, according to which the gynandromorph arises from an egg in which one of the two first cleavage nuclei unites with a sperm, is disproved, according to Cockayne "by the existence [in certain Lepodoptera] of perfect halved gynandromorphous hybrids both sides of which show equal admixture of the characters of both parents." Morgan has more recently endeavored to account for gynandromorphs in *Drosophila* as due to a lagging sex-chromosome. As a full account of his researches has not yet been published, I am unable to undertake the task of harmonizing it with what I conceive to be the conditions in the Formicidæ.

¹ Ueber die Entstehung der Eugsterschen Zwitterbienen Arch. Entwickl. Mech., Org. 41, 1915, pp. 264-311, 2 pls.

² Ueber die Gynandromorphen Bienen des Eugsterschen Stockes. Verhandl. phys. med. Ges. Würzburg 43, 1915, pp. 173-230, 8 pts.

³ "Gynandromorphism" and Kindred Problems. Journ. Genet. 5, 1916, pp. 75-129, 5 pts.